

BEHAVIORAL INTERACTIONS OF BLUE-WINGED AND GOLDEN-WINGED WARBLERS

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The interactions of populations in recently established zones of secondary contact are of interest from many points of view (Mayr 1963). The degree of hybridization will determine the future evolutionary independence of the 2 populations (Mayr 1963, 1970; Short 1969), and the degree of ecological overlap and competition will affect their future coexistence in the same community (Lack 1944, 1971). These long-term evolutionary and ecological consequences are mediated through daily behavioral interactions that are based, in part, on what is often called "species discrimination." If individuals fail to discriminate in selecting mates (Sibley 1957, Mayr 1963) or in establishing territories (Murray 1971), and if the failure to discriminate is reproductively disadvantageous, there will be selection for greater discrimination in responding to different phenotypes.

The behavior of hybridizing populations has been increasingly studied (Ficken and Ficken 1967, 1968a,b, 1969; Gill and Murray 1972a,b; Kroodsma 1974; Emlen et al. 1975) with the development of the "play-back experiment." Species-specific characteristics sometimes occur in combination in hybrid individuals, the study of which may provide clues to the nature and effectiveness of isolating mechanisms.

We have already presented the results of our experimental work on hybridizing Blue-winged (*Vermivora pinus*) and Golden-winged warblers (*V. chrysoptera*) in southern Michigan (Gill and Murray 1972a,b). The present paper reports the behavior of these warblers in natural circumstances, especially their intraspecific and interspecific aggression. Some of our results bear on the ontogeny of species discrimination and on the nature of hybridization between these species.

METHODS

We studied marked individuals in 1969, 1970, and 1971 in 2 areas of Michigan: Island Lake Recreational Area near Brighton, Livingston County, and near Burke Lake in the Rose Lake Wildlife Research Area in Clinton County, about 16 km east-northeast of Lansing (Ingham Co.). These 2 sites are about 60 km apart.

Blue-winged are more numerous than Golden-winged warblers but range into drier habitats. In wetter habitats where Golden-winged Warblers are most common, both species occur in equal abundance.

In 1969 we observed the birds almost daily from 5 May through 24 June at Island Lake, and on only 3 days at Burke Lake. In 1970 we began observations on 30 April at Island Lake and on 3 May at Burke Lake. FBG noted activity primarily at Island

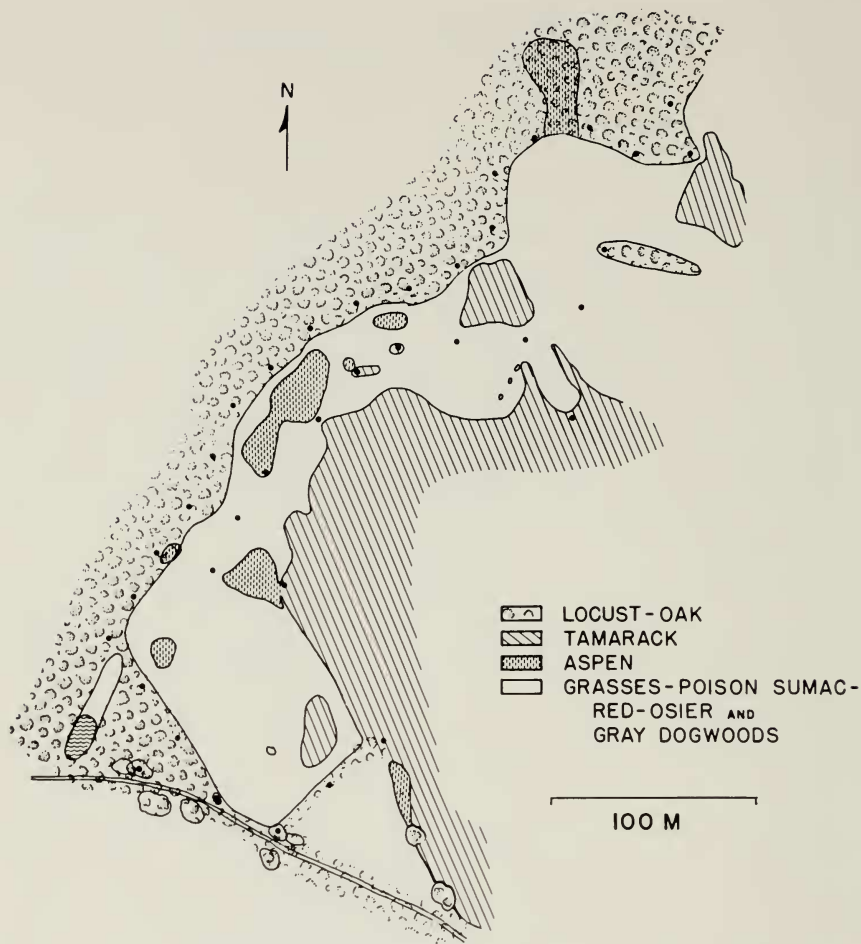


FIG. 1. Habitat map of the main study area at the Island Lake Recreational Area.

Lake while engaged in experimental work, while BGM concentrated on mapping territories, dividing his time about equally between both areas. We were in the field almost daily throughout May. In June BGM continued daily observations at Burke Lake and made 3 visits to Island Lake. In 1971 BGM began observations at Burke Lake on 28 April and continued almost daily observations there through May, while visiting Island Lake only once.

Additional but casual observations (with respect to data presented in this paper) were made in surrounding areas, especially in Hartland Township, Livingston County.

For our work on territoriality we concentrated on 2 small areas that were each occupied by about 12 individuals. The Island Lake area (Fig. 1) is a narrow, low

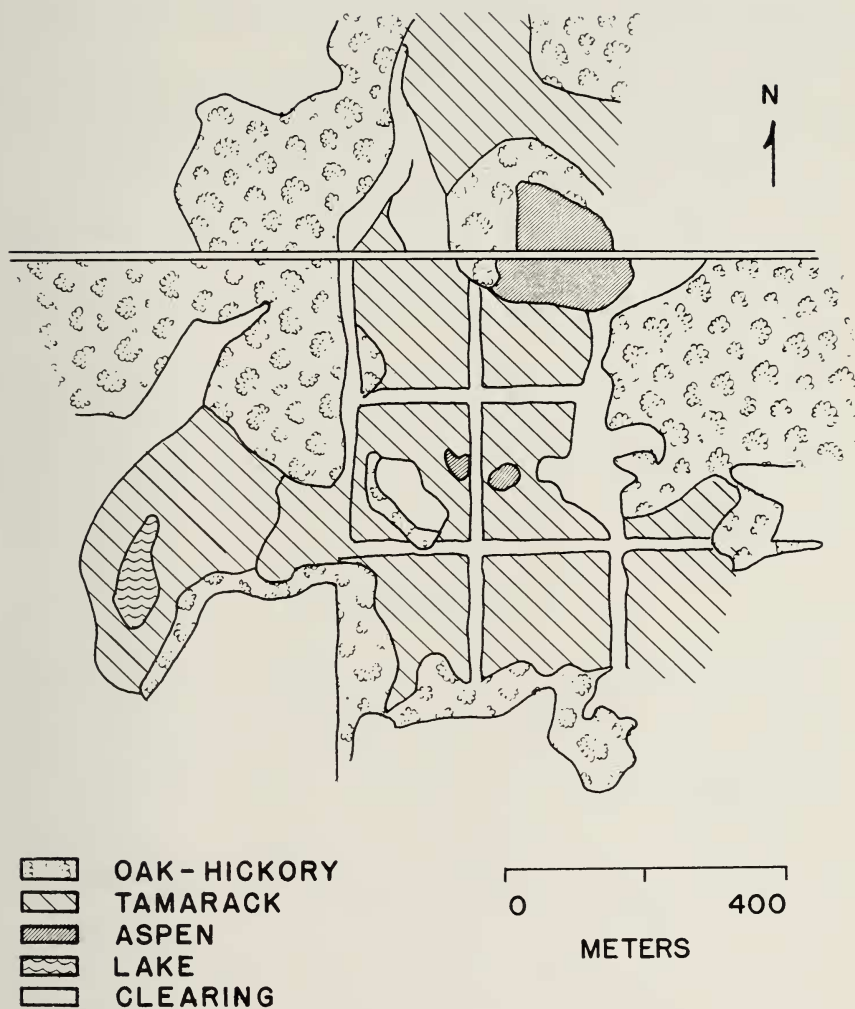


FIG. 2. Habitat map of the main study area near Burke Lake on the Rose Lake Wildlife Research Area. The map is drawn from one provided by Gordon Zorb of the State of Michigan Department of Wildlife Resources.

swamp of tamarack (*Larix laricina*), poison sumac (*Rhus vernix*), red-osier and gray dogwoods (*Cornus stolonifera* and *C. racemosa*), and poplars (*Populus deltoides*). It is bordered on the west by a dry upland deciduous forest of oaks (*Quercus* spp.) and locust (*Robinia pseudo-acacia*); on the east by a tamarack forest bordering the Huron River. We mapped this area by laying out 2 transects marked at 30.5 m intervals and by triangulation.

The Burke Lake area (Fig. 2) is an extensive tamarack swamp surrounded by

higher, drier oak-hickory woodlands. The swamp is crisscrossed by several man-made clearings, which we used as trails. The forest has been thinned in recent years as a result of the larch sawfly (*Pristiphora erichsonii*).

We color-banded almost all the males occupying these areas. A few birds were mist-netted by simply setting nets in likely spots. Our usual technique was to attract a selected bird to a net by using both models and tape-recorded songs. We were able to net most birds within 30 min. In addition to banding the birds with a Fish and Wildlife Service aluminum band and 2 colored, plastic bands, we examined each bird for signs of introgression according to criteria established by Short (1963) and slightly modified by us (Gill and Murray 1972b).

In the text we refer to individuals by the initials of the species name and the color of the bands. For instance, B-RW refers to a Blue-winged Warbler with 1 red band above 1 white band.

Each individual's activity was plotted on a composite map, and a line was drawn around the activity points. We calculated the area of a territory by tracing the territory onto graph paper and counting the squares. We saw few intraspecific encounters at these boundaries. Nevertheless, we think the boundaries of these activity spaces accurately delineate territories because from our experimental work we know that within these areas a particular male responds aggressively toward playbacks of intraspecific song.

RESULTS

Arrival

Male Blue-winged and Golden-winged warblers arrived in southern Michigan in late April and early May. In both 1969 and 1970 at Island Lake some resident male Blue-winged Warblers were already on territory when we began observations on 5 May and 30 April, respectively, but both Blue-winged and Golden-winged warblers continued to arrive throughout May and even into June (Table 1). A few Blue-winged Warblers arrived only slightly earlier than did Golden-winged Warblers. There appears to be broad overlap in arrival dates of these 2 species.

The same was observed at Burke Lake, where our coverage was not so intense as at Island Lake except in 1971. Then, with almost daily coverage from 28 April on, the first 2 Blue-winged Warblers arrived on 6 May, and the first Golden-winged Warbler on 7 May. Arrivals of banded birds were: G-RW, 7 May; Lawrence's (L-RR), 10 May; G-GR, 11 May; Brewster's (Br-YY), 13 May*; G-YG, 14 May; G-GW, 15 May; B-GR, 20 May*; and G-RP, 22 May*. (Starred birds may have arrived, at most, one day earlier.)

We have reported here and in Table 1 only those birds whose appearance we are certain about because of the intensity of our coverage of a particular area, the distinctiveness of an individual's song, and our use of color bands.

Some of the later "arrivals" may have moved in from surrounding areas rather than having just returned on migration from their winter range.

TABLE 1
ARRIVAL DATES OF TERRITORIAL *VERMIVORA* AT ISLAND LAKE RECREATION
AREA, MICHIGAN^a

	1969	1970
Blue-winged Warblers		
B-RR	5 May	—
B-WW	5 May (+1) ^b	1 May
B-BB	5 May (+1)	1 May
B-GG	5 May (+7)	1 May
B-GY	31 May	—
B-BG	9 June	—
B-RG	(banded 7 June)	30 April
B-YY	13 May (+14) ^c	—
B-WG	—	3 May ^d
B-YR	—	4 May ^d
B-BY	—	11 May ^e
B-BW	—	14 May ^e
B-WB	—	18 May
Golden-winged Warblers		
G-YY	7 May ^f	—
G-RR	7 May ^f	(between 12 and 19 May)
G-GG	7 May	4 May
G-BB	4 June (+3)	—
G-BY	—	11 May ^e
G-WR	—	18 May (+1)
G-RG	—	20 May (+1)
G-RY	—	21 May (+1)

^a Observations began on the morning of 5 May 1969 and late afternoon of 30 April 1970.

^b Number in parentheses indicates the number of days later that a bird was banded.

^c Distinctive song.

^d At another closely watched site.

^e May have been present the previous day when we did not cover area.

^f One of these was present on 5 May.

Territorial Establishment

During the first week or so after arrival, male Blue-winged and Golden-winged warblers usually sing infrequently and respond poorly to playback. We could have passed these birds over as transients had they not been marked. At this time most birds restricted their activity to those areas where they later became more conspicuous in their singing, display, and aggressiveness.

As territories were being established, there were some changes in the area occupied by some birds, more so by Golden-winged Warblers. In 1969 at Island Lake one Blue-winged Warbler (B-BB) was first netted over

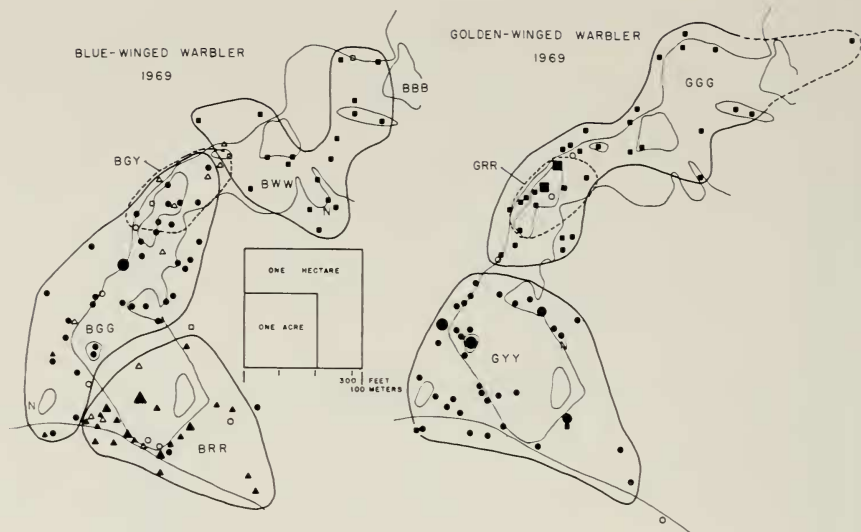


FIG. 3. Territories of Blue-winged and Golden-winged warblers at Island Lake in 1969. The territories are indicated by the heavy lines superimposed over the lighter lines outlining the major features of the habitat (see Fig. 1). The activity of each individual is shown by symbols: B-RR, triangles; B-GG, circles; B-WW, squares; G-YY, circles; G-GG, squares. There are two exceptions: only the outline of the territory is shown for B-GY and for G-RR, represented by dashed lines. Blackened symbols represent observations of singing birds, and the white symbols represent observations of non-singing birds. The larger symbols represent many observations at a single singing perch. The "N" indicates the position of the nests.

180 m from where he finally established his territory. A Golden-winged Warbler (G-RR) sang regularly from 7 to 12 May at Island Lake before it inexplicably disappeared. FBG found him in 1970 on the east side of the Huron River, about 400 m away. At Burke Lake in 1970 we banded a Golden-winged Warbler (G-RW) in another's (G-GR) territory, and another Golden-winged Warbler (G-GW) near the boundary of G-RW's territory, neither of which was seen in these spots again. In 1970 G-GG returned to Island Lake on 5 May and sang throughout the area before disappearing on 15 May. So far as we know he was never challenged. He was subsequently replaced by 2 new Golden-winged Warblers, G-RG on 18 May and G-WR on 20 May. Both remained at least until we last visited the area on 18 June. On 22 May 1970 at Island Lake we accidentally killed a Golden-winged Warbler that was first detected the previous evening. Within an hour he was replaced by another Golden-winged Warbler that sang from the same singing perches.

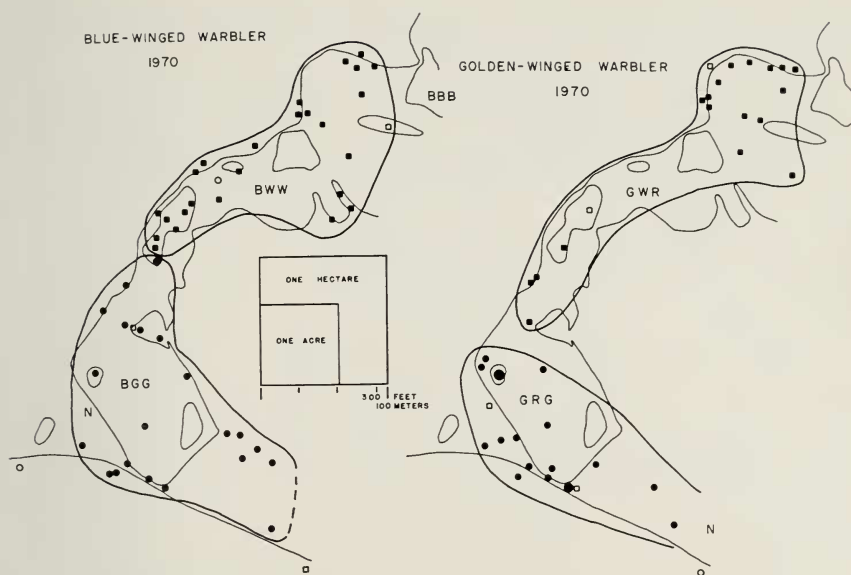


FIG. 4. Territories of Blue-winged and Golden-winged warblers at Island Lake in 1970. The symbols are the same as in Fig. 3, except that the Golden-winged Warblers are different birds. In 1970 G-GG sang throughout the area before disappearing just before the arrival of G-RC and G-WR.

Territory establishment continued through late May and early June. Later arrivals must either establish territories in peripheral, unoccupied areas or challenge already established territory holders. We observed both. The earlier arrivals (Table 1) occupied the central areas (Figs. 3 to 5), whereas most later arrivals occupied the periphery. We did observe 2 major challenges to territory holders in the swamp area. At Island Lake on 31 May 1969 a new male (later banded B-GY) appeared in B-GG's territory. After about one hour's encounter of continuous singing of muted Type I and Type II songs and chasing, B-GY established a small territory from which he excluded B-GG (Fig. 3), where he remained at least until we ceased observations in late June. On 9 June 1969 we watched another prolonged encounter, this time between B-RR and an intruder (later banded B-BG). B-BG apparently established dominance over B-RR because the former sang for a half hour or so without interruption and B-RR was unobserved. We set up a net and caught B-BG, unfortunately while he was being chased by B-RR who had reappeared. B-BG was not seen again, perhaps because of our interference.

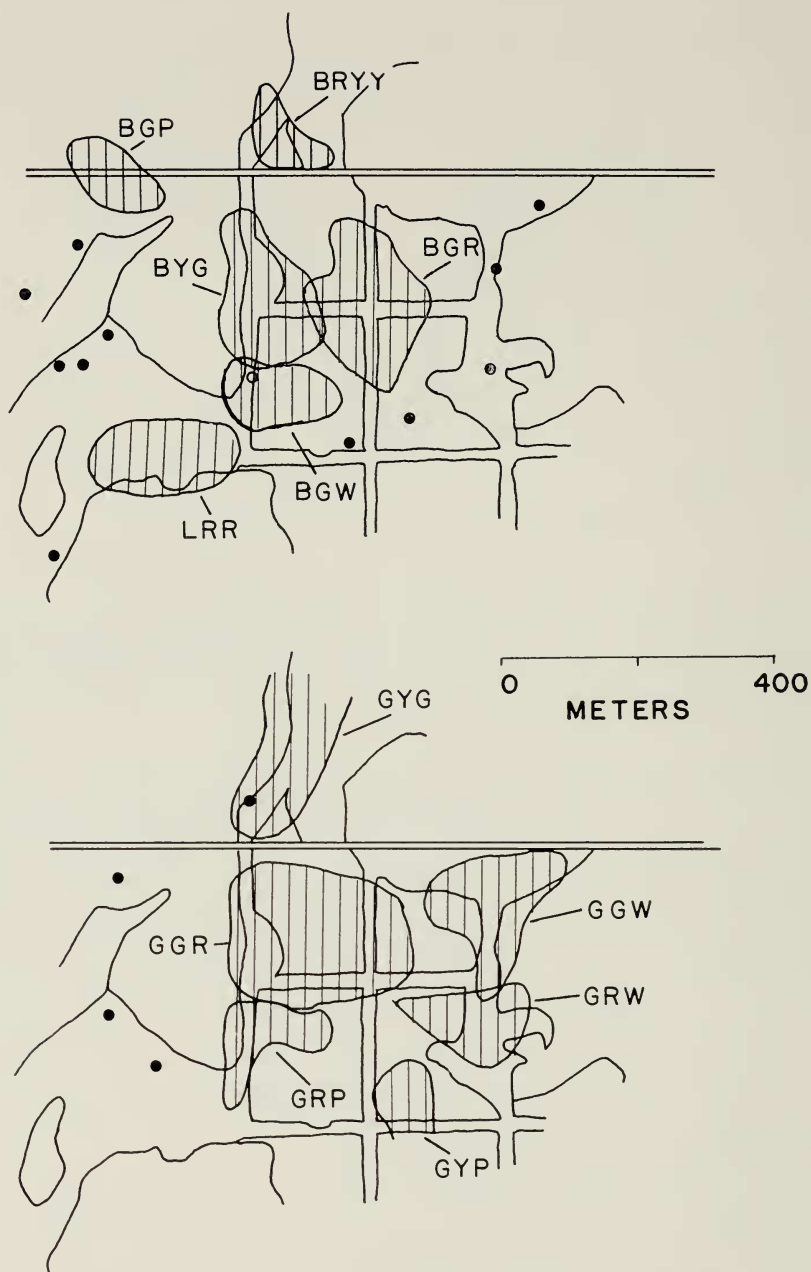


FIG. 5. Territories of *Vermivora* at the Burke Lake area in 1970. The territories are shaded areas superimposed over light lines outlining the major features of the habitat (see Fig. 2). The black dots represent sightings of unmarked Blue-winged Warblers (upper) and Golden-winged Warblers (lower).

TABLE 2
TERRITORY SIZE (HECTARES) OF *VERMIVORA* IN MICHIGAN

Blue-winged Warbler			Golden-winged Warbler		
Island Lake					
	1969	1970		1969	1970
B-RR	1.5	—	G-YY	2.4	—
B-GG	1.9	2.1	G-GG	2.0	—
B-WW	1.3	1.6	G-RG	—	1.6
G-GY ^a	0.4	—	G-WR	—	1.7
Burke Lake					
B-GR	—	3.0	G-GR	—	5.2
B-YG	—	2.6	G-GW	—	2.6
B-GW	—	1.5	G-YG	—	2.4+
B-GP	—	1.1	G-RW	—	1.6
			G-RP	—	1.4
			G-YP	—	0.8+
Lawrence's Warbler			Brewster's Warbler		
		2.2			0.9

^a Established territory on 31 May in a portion of B-GG's territory.

Spatial Relationships

Blue-winged, Golden-winged, Brewster's, and Lawrence's warblers maintained typical Type A territories (Nice 1941) to which the males confined most, if not all, of their activities. As mentioned earlier, the territories of Blue-winged and Golden-winged warblers overlapped extensively (Figs. 3 to 5). The hybrids did not overlap with birds singing the same song—in these cases, the Blue-winged Warbler song. There was, however, a tendency for Blue-winged and Golden-winged warblers to sing primarily from different singing perches, as previously noted by Ficken and Ficken (1968a), despite our observations of individuals of both species at times singing near each other without apparent conflict. At times early in the season we did observe newly arrived Golden-winged Warblers to cause a shift in the singing perches of already established Blue-winged Warblers. This separation of primary singing areas within mutually held territories deserves further study.

Territories in Michigan are large, ranging from 1.3 to 5.2 ha (Table 2). At Island Lake where our measurement of territory size was more accurate than at Burke Lake, the average size of a Blue-winged Warbler territory was 1.8 ha and of a Golden-winged Warbler territory, 1.9 ha. At Burke

Lake territories averaged 2.0 to 2.7 ha, respectively, for Blue-winged and Golden-winged warblers.

At Island Lake we occasionally saw a Blue-winged Warbler or a Golden-winged Warbler trespassing on adjacent territories (Figs. 3 and 4). Sometimes a bird would be over 400 m from its own territory. These trespassing birds rarely sang and then never more than a few songs. One Golden-winged Warbler (G-YY) left his territory apparently to watch a fight between 2 Blue-winged Warblers on 31 May 1969.

We observed one other unusual incident. On 12 June 1969 we found B-RR singing normal Type I songs from near the center of his territory. He finally flew off and disappeared in the direction of B-GG's territory. After about 5 min he returned to his singing perch. This behavior was repeated several times during the next hour. We followed him and found that he was singing muted Type I songs at the southern edge of B-GG's territory, where a female Blue-winged Warbler was completing a nest. He swooped down at her on a 45° angle to the nest site and then returned to the center of his territory, where he continued singing normal Type I songs. Either B-RR was courting B-GG's female or his female was building in B-GG's territory. Whatever the case we did not see B-RR at this spot again, and a few days later the nest was deserted.

At Burke Lake each male restricted all of his activities to within his territory's boundaries. The only trespassing we recorded was by newly arrived birds; at least we sometimes originally caught a bird outside the area in which he subsequently established a territory.

By plotting activity spaces at Island Lake for each week in 1969 (Fig. 6) we note that the apparent activity space for each individual changes, which might imply changes in the boundaries of territories. These changes, though, seem to be the result of the males changing the places from which they sang most frequently because the entire season's activity spaces barely overlap (Fig. 3). If territory boundaries shifted during the season, we would expect to see broad overlap in the birds' seasonal activity spaces, as is the case in the one proved territory boundary change—B-GY's encroachment of B-GG's territory (Figs. 3 and 6). Such results emphasize the need for long-term intensive observation in studies of territorial behavior in birds.

Territorial Aggression

In natural encounters between Blue-winged Warblers, between Golden-winged Warblers, and interspecifically, the form in which aggression was expressed is characterized only by its diversity. Encounters varied in length from a few seconds to at least an hour, in activity from simply sing-

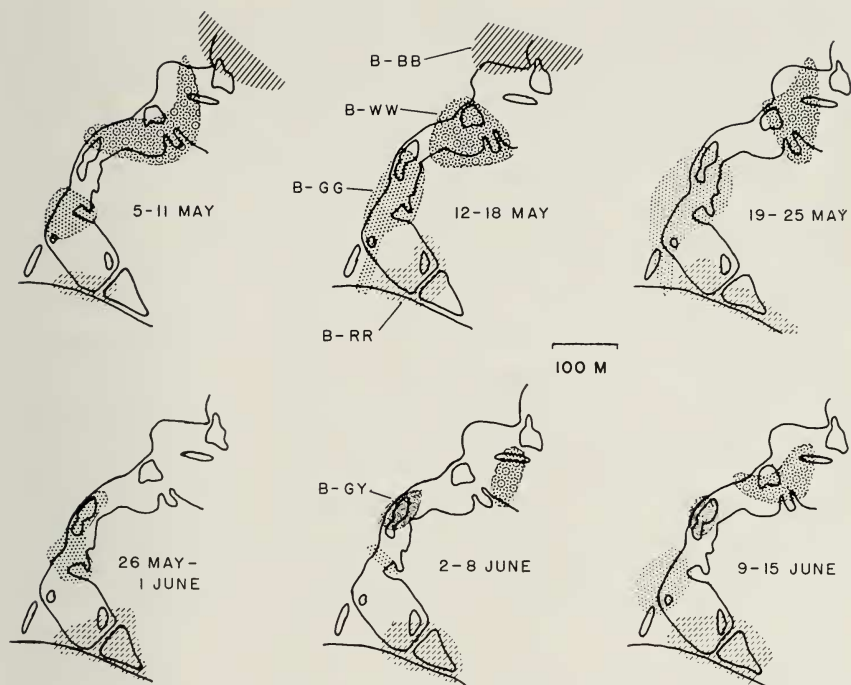


FIG. 6. Week by week "changes" in the mapped territories of Blue-winged Warblers at Island Lake in 1969. B-GY's activity on 31 May and 1 June is not included but was restricted to the area indicated for 2 to 15 June.

ing at each other while remaining relatively motionless to vigorous "supplanting," "flying past," or "fighting" (the terms are fairly descriptive and have been defined by Ficken and Ficken 1968a), and in associated vocalizations from chip notes to primary and secondary songs (either one or another or both) at different intensities (either muted or normal).

In order to demonstrate this diversity we describe below several of these encounters.

Between Blue-winged Warblers.—On 8 May 1969 at Island Lake B-BB was singing Type I songs when an unbanded Blue-winged Warbler sang Type II songs. B-BB gave chase with loud chips and buzz-chips almost landing on the other bird before being repulsed. Immediately both birds began foraging quietly.

On 20 May 1969 B-RR and B-GG engaged in a long encounter in an area that we have mapped as part of B-GG's territory. It began with B-RR chipping near a female Blue-winged Warbler. B-GG appeared

without a sound, and the chase began, in circles and up and down through the trees with B-GG doing most of the chasing. Only chips were given by both birds until they disappeared. Then, B-GG reappeared and gave 3 muted primary songs with long intervals between. B-RR came back and was immediately chased by B-GG. Then, B-RR returned and gave 3 primary songs. We did not see B-GG, and the encounter ended.

Later, on 23 May these birds battled again. B-GG began singing Type II songs, which were answered by B-RR singing Type II songs. There followed a series of buzz-chips but the birds could not be seen. Finally B-GG disappeared, and B-RR started singing Type II songs again. (We mapped this spot as part of B-GG's territory because B-RR was seen here and in surrounding areas only rarely compared with B-GG.)

On 31 May 1969 at Island Lake we observed a new arrival (later banded B-GY) establish a territory in the northern portion of B-GG's territory. This encounter lasted over 45 min. It consisted of vigorous chasing and flying past with few direct supplanting attacks. Both birds sang and called continuously a mixture of muted Type I songs, Type II songs, and chips. Finally B-GG left the area, and B-GY took full possession, singing normal Type I songs. (At one time BGM was watching the encounter across a small clearing from G-YY, who was also watching the encounter, and incidentally was far outside his own territory.)

We observed a similar encounter on 9 June 1969 at Island Lake between B-RR and another intruder (later banded B-BG). We thought this encounter had the same result because B-BG was finally singing normal Type I songs without interruption by B-RR. We put up a net and caught B-BG, unfortunately when he was being chased by B-RR, who had apparently only taken a rest. B-BG disappeared, and B-RR continued singing muted Type I songs and Type II songs.

On 19 May 1970 at Burke Lake only Type I songs were heard in a singing duel between B-YG and another Blue-winged Warbler.

Between Golden-winged Warblers.—On 31 May 1970 at Burke Lake G-GR and G-RP engaged in a vocal duel at the boundary of their territories. For almost 12 min the 2 birds sang near each other, each singing muted and shortened (2 or 3 notes) Type I songs. There was no chase. Eventually they both moved off toward the centers of their territories, singing louder. As they moved apart G-RP attacked a male Cerulean Warbler (*Dendroica cerulea*).

On 27 May 1970 at Island Lake an incident occurred that involved G-RG, G-WR (which sang Blue-wing songs), certainly another but unidentified Golden-winged Warbler, and an unidentified Blue-winged Warbler. G-RG was singing Type I songs from within his territory but began chipping

and chased a bird into the shrubbery. A Blue-winged Warbler appeared and departed. Then G-RG began singing Type I songs again. Another Golden-winged Warbler, not seen, began singing Type I songs. Both stopped. There followed a long bout of Type II songs, which ended with a chase, the second bird this time being G-WR outside his territory. Upon G-WR's departure, G-GR again began singing Type I songs.

Between Golden-winged Warblers and Blue-winged Warblers.—As reported by Ficken and Ficken (1968a) and by us elsewhere (Gill and Murray 1972b), male Golden-winged and Blue-winged warblers by and large ignore each other. We did observe, however, on several occasions aggressive interaction between these species, most of which were of short duration (a few seconds). All encounters involved the displays and vocalizations described above for intraspecific encounters. At least one male Golden-winged Warbler (G-GR at Burke Lake) was persistently and vigorously aggressive toward Blue-winged Warblers. A Blue-winged Warbler (B-YG) established a territory that was almost entirely overlapped by G-GR's (Fig. 5). Whenever B-YG sang Type I songs from the central portion of his territory he was attacked within a minute or so by G-GR. Eventually B-YG became quite inconspicuous, singing infrequently and only on occasion being detected by us.

Another Blue-winged Warbler (B-GR) became increasingly aggressive toward G-GR as the season progressed, but his territory was largely outside G-GR's (Fig. 5). On 17 May 1970 we observed B-GR sitting or foraging silently while nearby G-GR sang Type I songs for 15 min. As soon as G-GR moved away, B-GR began singing Type I songs. By 31 May B-GR was equally as aggressive as G-GR, and they could be seen almost any evening after that in aggressive encounters. Encounters in the morning were rare.

On another occasion a territorial Blue-winged Warbler (B-GP) remained silent while an unbanded Golden-winged Warbler sang from the former's usual singing perch.

In 1971 at Burke Lake, G-GR was challenged by 2 different Blue-winged Warblers. When he returned on 11 May a new Blue-winged Warbler had already established a territory that included G-GR's major 1970 singing perches. This area was disputed with G-GR subordinate but persistent until 14 May when he appeared to have established dominance, the Blue-winged Warbler moving to an adjacent area. On 20 May (BGM missed 2 days) B-GR had returned and was definitely dominant over G-GR. B-GR was singing loudly both song types without interference, and G-GR sang only occasionally. On 22 May, G-GR had re-established dominance in his territory, with B-GR moving slightly to the east, where he was apparently

tolerated by G-GR. In 1970 B-GR would have been chased from this area by G-GR.

Of particular interest is a series of encounters between a Blue-winged Warbler (B-WW) and a bird (G-WR) with Golden-winged Warbler plumage (hybrid index 14) but Blue-winged Warbler Type I song and Golden-winged Warbler Type II song (see Table 1 and Fig. 3 in Gill and Murray 1972a). On 1 May 1970 B-WW established a territory in the area he held in 1969 (Figs. 3 and 4), and on 18 May G-WR arrived on B-WW's territory. Murray observed this bird (G-WR) and B-WW from 07:50 through 09:45. During this time G-WR sang from aspens and oaks bordering a swampy opening. Three times B-WW flew into G-WR's tree from a spot over 100 m away. B-WW flew from branch to branch within the tree, singing Type I songs all the while, for 5 to 15 min before leaving the tree. Within 30 min B-WW returned to the tree and repeated his previous performance. Evidently B-WW was responding to G-WR's Blue-wing-like song Type I but did not respond to G-WR's Golden-wing-like plumage. B-WW never seemed to locate the singer because he never approached G-WR closely. Instead he moved about within the tree, appearing to be searching for the singer, which normally would have a Blue-wing-like plumage. Normally, a response to Type I song leads to a "supplant" or "chase" of the intruder.

G-WR completely ignored B-WW's presence, at least there was no observable change in his behavior after B-WW arrived in the tree or after he departed from the tree.

When away from the tree B-WW was usually quiet and evidently nervous (before he discovered G-WR's presence Murray remarked in his field notes on B-WW's unusual behavior).

On 20 May Gill was observing B-WW foraging and chipping when G-WR began singing Type I songs nearby. B-WW immediately froze, into "study behavior," sitting motionless and only occasionally singing muted "bee" notes of the Type I song. G-WR left shortly, and B-WW moved off.

On 20 May Murray did see G-WR "chase" a Blue-winged Warbler, which probably had intruded G-WR's individual distance. As G-WR was foraging quietly in the top of a little oak, an unbanded and quiet Blue-winged Warbler (probably a female) moved upward through the tree with several short flights. It directly approached G-WR, who responded by "supplanting." The Blue-winged Warbler moved about 3 m and was again "supplanted" by G-WR, flying to the other side of the tree. It then flew away.

On 28 May Gill observed both G-WR and B-WW singing loud Type I

songs within 10 m of each other for nearly 5 min. There was no interaction, both birds giving the appearance of coexistence without conflict.

The responses of both B-WW and G-WR to Blue-wing and Golden-wing Type I and Type II songs were tested experimentally with playbacks of tape-recorded songs (see Gill and Murray 1972b for details). B-WW did not respond to Golden-wing Type I but responded strongly to Blue-wing Type I and both Blue-wing and Golden-wing Type II songs. We interpreted this as indicating an ability to discriminate species by their Type I songs but not by their Type II songs (Gill and Murray 1972b).

The response of G-WR provided a surprise. On 18 May Gill's first playback was a Golden-wing Type I song, "heterospecific" to its own song type, to which G-WR responded strongly. A second test on 19 May presented the sequence: at 08:00, Blue-wing Type I followed by Golden-wing Type I; at 08:45, Blue-wing Type II followed by Golden-wing Type II. In each experiment G-WR did not respond in any way to Blue-winged Warbler songs and responded strongly to both types of Golden-winged Warbler songs.

On 21 May Gill played back to G-WR a recording of his own Type I song without response.

An experiment on 29 May had B-WW responding strongly to playback of Blue-winged Warbler Type I songs while ignoring, or not responding to, G-WR, which was singing Blue-wing Type I songs about 30 m away. This differential response of B-WW to Blue-wing Type I songs is consistent with his behavior of the previous day when both B-WW and G-WR were singing near each other without conflict.

Unfortunately we did not play back G-WR song to B-WW.

Encounters involving hybrid phenotypes.—On 10 June 1969 two birds were singing Type II songs near Burke Lake. Finally a Blue-winged Warbler flew away. The remaining bird was a Lawrence's Warbler.

On 12 May 1970 at Island Lake a Brewster's Warbler appeared in B-BB's territory, giving loud chips. B-BB responded by giving 2 muted Type I songs and chasing the Brewster's Warbler briefly. The Brewster's Warbler moved off, and B-BB sang a few more Type I songs.

On 27 May 1970 near Island Lake a Brewster's Warbler (Br-RR) was singing Blue-wing Type I songs from an exposed perch about 13 m above the ground. A Golden-winged Warbler (G-WW) that had been singing across a clearing came closer and eventually took a position 6 m directly above Br-RR, who took no notice of G-WW until the latter attacked by diving (Diving Attack of Meyerriecks and Baird 1968). Br-RR dropped straight downward into the brush with G-WW not far behind. No other activity or sound was noted for 15 min after the attack.

Aggression with other species.—Blue-winged and Golden-winged warblers engaged in brief encounters with individuals of a wide variety of other species. In almost all cases, the former were the aggressors. We saw male Blue-winged Warblers chase a female Cerulean Warbler, a Magnolia Warbler (*Dendroica magnolia*), and an American Goldfinch (*Spinus tristis*), which however did not move. Blue-winged Warblers were chased 3 times by goldfinches and supplanted once by an Indigo Bunting (*Passerina cyanea*).

Male Golden-winged Warblers attacked a Cerulean Warbler, Northern Parula (*Parula americana*), Chestnut-sided Warbler (*Dendroica pensylvanica*), Yellowthroat (*Geothlypis trichas*), Indigo Bunting (both male and female), a goldfinch (without effect), Field Sparrow (*Spizella pusilla*), and Red-eyed Vireo (*Vireo olivaceus*). We saw none of these species or any other species chase Golden-winged Warblers.

Reproductive Behavior

The courtship sequence begins with a female Blue-winged or Golden-winged warbler approaching a singing male. Typically, the male is singing Type I songs from a perch in a tree, and the female is lower in the underbrush, often giving "Buzz-chip" notes (= *Tzip* of Ficken and Ficken 1967) that closely resemble the location and begging notes of fledglings. The male stops singing, stares intently downward at the female, and finally dives at and chases her. Subsequent interactions between the male and female are variable and include Bill Duelling, Gliding, and Moth Flight, as well as Soliciting and Copulation (see Baird 1967, Ficken and Ficken 1968b).

We observed what appeared to be ritualized Nest Site Prospecting in one pair of Blue-winged Warblers and one pair of Golden-winged Warblers. The male leads the female from one clump of vegetation to another. The male flies between clumps with a Moth Flight and after landing, pivots slowly around his perch like a mechanical toy with feathers fluffed (see Baird 1967) about 180° until facing the female, who is investigating the previous clump.

We did not observe courtship feeding, but BGM did see a male Golden-winged Warbler feed a female, who was sitting on a nest with recently hatched young, several times within one hour.

Nest Site Location

All 6 nests that we were able to find were located at the periphery of a male's territory rather than near the center (Figs. 3 and 4). Males rarely, if at all, sang in the vicinity of the nest once incubation was underway.

TABLE 3
RETURNS OF BANDED MALE *VERMIVORA* IN MICHIGAN

	Island Lake			
	1969 Banded	1970		
		Returned		Returned
Blue-winged Warbler	10			5 ^a
Golden-winged Warbler	5			3
Brewster's Warbler	1			1

	Burke Lake			
	1969 Banded	1970		1971
		Returned	Banded	Returned
Blue-winged Warbler	0	—	5	1
Golden-winged Warbler	0	—	6	5 ^b
Brewster's Warbler	1	0	1	1
Lawrence's Warbler	1	1	0	1

^a Includes one bird rediscovered in 1970, 10 km from place of banding.

^b Includes G-R, assumed to be G-RP.

Return Rates of Adults

The survival of adults from one year to the next is difficult to estimate. One male disappeared in 1969 only to be found nearby in 1970 when we expanded coverage into a new area. Even more surprising was the discovery of another male about 9.6 km distant from its 1969 territory. Considering only those birds in our intensively studied areas, the return rate was about 60% (Table 3), virtually the same as that reported by Mayfield (1960) for the Kirtland's Warbler (*Dendroica kirtlandii*). If we include the more distant returns, the survival rate of adults would be higher.

DISCUSSION

Basically our results confirm those of Ficken and Ficken (1968a) regarding the fact that male Blue-winged and Golden-winged warblers treat each other as distinct species and thus have largely overlapping territories where they occur together. We also agree that singing perches within mutually held territories tend to be separate though certainly not exclusive. Because we watched more birds than the Fickens did, we discovered that on occasion males do engage in persistent interspecific aggression, that is, some males of one species treat the males of the other species as if they were conspecific. This should not be too surprising inasmuch as we already know that the males and females of these hybridizing species sometimes respond to members of the other species as conspecifics.

In details our observations differ from those of Ficken and Ficken, who studied both species in central New York. These differences may reflect actual differences between geographically separate populations, or they may reflect the fact that our sample sizes are larger, our observations on some but certainly not all aspects were more intense, and we studied marked individuals.

For instance, Ficken and Ficken (1968a) state that "territories were roughly mapped by observing the positions of males for at least two days and usually over a period of several weeks," that the "Size of territories varied from less than one acre to almost two acres," and that "Both sexes confined all their activities to the territory from the time of arrival until the young were fledged." With our marked birds we found the territories of both the Blue-winged and Golden-winged warblers to vary between 1.3 and 4.9 ha (Table 2). We believe that had we not banded B-WW we could have easily considered his territory in 1969 to have been occupied by 2 males, one on either side of the wall of tamaracks and other trees that bisected his territory (Fig. 3). In another case, G-GG sang primarily in the southern portion of his territory and sporadically in the northern portion (Fig. 3). He certainly would have been considered 2 birds. Another Golden-winged Warbler (G-WR) had disjunct singing areas (Fig. 4), although we could have detected this because of his unique song.

As shown in Figures 3 and 4, some males at least were infrequent visitors to other males' territories, and surprisingly we saw B-RR courting a female building a nest in another male's territory, an event we could not have guessed by watching unmarked birds.

These and some other differences between the results of Ficken and Ficken and of ourselves cannot be resolved without further work with color-marked birds in other populations.

On the other hand some differences are undoubtedly real. Ficken and Ficken (1968a) state that "Song is usually absent during encounters and is only resumed after a few minutes, typically when one of the encountering birds has left the area." In Michigan aggressive encounters almost always included vocalizations. A particular encounter may have included one or more vocalizations, including normal Type I, muted Type I, Type II songs, and chips. In contrast to the situation in both New York and Michigan, Meyerriicks and Baird (1968) report that in Massachusetts "Singing was a predominant feature of the overall agonistic situation, but other vocalizations were remarkably infrequent" between a Brewster's Warbler and a Blue-winged Warbler.

The territories of Michigan Blue-winged and Golden-winged warblers are larger than those of other Blue-winged Warbler populations, which

averaged 1.0 ha on Long Island (Gill, unpubl. data) and under 0.8 ha in central New York (Ficken and Ficken 1968a), as well as those of most other parulid species that have been studied (summarized by Mayfield 1960: Table 4). An exception is the Kirtland's Warbler, whose measured territories averaged 3.4 ha.

The pattern of territorial establishment by arriving males, such as we noticed in these warblers, has been observed in a variety of other species, including some parulids (Ficken and Ficken 1962). Generally it seems that early arriving individuals establish themselves on better quality territories. The basis for this conclusion is primarily the tendency for peripheral males to shift to central territories when opportunities arise and in the greater fluctuations in occupation of peripheral territories (Brown 1969), because suitable measures of territory quality are rarely achieved.

The occurrence of interspecific aggression in natural situations confirmed our experimental results on interspecific discrimination using tape-recorded playbacks—81% did not respond to heterospecific song (Gill and Murray 1972b)—assuring us that this technique, used earlier by Gill and Lanyon (1964) and Ficken and Ficken (1969) is justified, at least in these species.

Interspecific aggression between Blue-winged and Golden-winged warblers did not result in mutually exclusive territories. In one case B-YG reduced his singing and conspicuousness greatly as a result of G-GR's persistent aggression, and thus each was able to maintain largely overlapping territories (Fig. 5). In the other case, B-GR and G-GR had established territories that only partially overlapped (Fig. 5). These 2 birds were more aggressive toward each other than any other pair of *Vermivora* territory holders.

We are unable to confirm any pattern to the aggression between both *Vermivora* species and other species that was reported by Ficken and Ficken (1968a). These interspecific encounters are more complex than any theory suggesting similarities of color or pattern can predict. The very few encounters between male Blue-winged and Golden-winged warblers and hybrid phenotypes we observed also did not confirm the suggestion of Ficken and Ficken (1968a) that facial pattern more than song type determined who was aggressive toward whom.

Species discrimination and hybridization

The study of avian vocalizations has focused on the ontogeny of the sounds themselves (Lanyon 1960, Marler 1964, Konishi and Nottebohm 1969), on the effects of vocalizations on conspecific receivers (Marler 1956, Weeden and Falls 1959, Falls 1963, 1969), and on whether indi-

viduals of hybridizing species could distinguish heterospecific from conspecific song (Lanyon 1957, Gill and Lanyon 1964, Ficken and Ficken 1967, Gill and Murray 1972b, Kroodsma 1974, Emlen et al. 1975). We ask the question: How does an individual of species A develop species-specific responses to the vocalizations of species A rather than to those of species B, C, or D? Or, more specifically: why do some Blue-winged Warblers and Golden-winged Warblers respond only to conspecific song and others respond to both conspecific and heterospecific song?

The behavioral interactions of B-WW and G-WR are of special interest in this regard, as they constituted a kind of natural experiment in which a living bird (G-WR) combined the species-specific signals of 2 species.

G-WR was a Golden-winged Warbler in plumage and Type II song and a Blue-winged Warbler in his Type I song. It responded selectively to vocalizations usually associated with its plumage type but not at all to its own song Type I. This indicates that the ontogeny of its species-specific vocalization is independent of the ontogeny of species-specific responses to species-specific vocalizations. Whatever are the genetic and environmental variables that influence the acquisition of species-specific song, they are not the same genetic and environmental variables that influence the development of responses to those songs, unless these are acting during different critical periods.

The behavior of the Blue-winged Warbler B-WW is also enlightening. B-WW responded aggressively to the Blue-wing-like vocalizations of the Golden-winged Warbler G-WR by flying toward the singing G-WR from a great distance (over 100 m). But this aggressive behavior was never reinforced by the presence of an intruder with the appropriate, aggression-stimulating visual signal—Blue-wing-like plumage. Eventually B-WW ceased responding to G-WR's song, while still responding aggressively to playback of Blue-winged Warbler song.

Generalizing, we suggest that an individual bird may come to recognize "species"—that is, respond selectively to conspecific individuals—by the responses it generates in conspecific and heterospecific individuals. One example, of many imaginable examples, is the following: an inexperienced bird responds to a variety of similar stimuli in its environment, both appropriate and inappropriate. Response to appropriate (species-specific) stimuli results in a species-specific sequence of behavior, whereas response to inappropriate (not species-specific) stimuli does not because the inappropriate signaler does not respond to the signals given by the inexperienced bird. Because of this differential response from appropriate and inappropriate signalers, the inexperienced bird learns to respond only to appropriate (conspecific) signalers.

Such a notion is consistent with our interpretation of the difference in responsiveness of different Blue-winged Warbler populations to heterospecific songs (Gill and Murray 1972b). The Long Island population (Gill and Lanyon 1964) and Maryland population (Ficken and Ficken 1967) are more responsive to playback of Golden-wing song, where Golden-winged Warblers are rare, than are the Michigan populations (Gill and Murray 1972b), where Golden-winged Warblers are abundant. We suggested that Blue-winged Warblers are less responsive to playbacks of Golden-winged Warbler songs in Michigan than in areas of allopatry because, where sympatric, they have an opportunity to respond to acoustic signals which are similar to their own acoustic signals, but which usually do not lead to appropriate species-specific sequences of behavior (i.e., aggressive encounters) because of their distinctive plumages.

Nevertheless, species discrimination breaks down from time to time, even between species that seem sufficiently different to prevent mixed matings. A contributing factor may be the rarity of one species (Mayr 1963), especially as it expands its range into the range of another species. Mixed matings produce hybrids, if they produce any offspring, and these hybrids are intermediates, which may respond to either one of the parental species or to both. Hybrids, then, can provide noise in a system in that they might interfere with normal development of species-specific responses of progeny of matings between conspecifics. For instance, a Brewster's Warbler singing a Golden-wing song might combine a visual, aggression-stimulating cue of one species and an acoustic, aggression-stimulating cue of the other species, and it might respond aggressively toward either one or perhaps both of the parental types. An inexperienced progeny of conspecific parents could learn to respond to non-species-specific cues as a result of an interaction with a hybrid. Many combinations of events are imaginable, and this may explain the diversity of aggressive interactions we observed: a non-singing Brewster's Warbler was attacked by a singing Blue-winged Warbler; a Golden-winged Warbler attacked a Blue-wing-singing Brewster's Warbler, which in no way responded to the approaching Golden-winged Warbler until it fled from the direct attack; mutual aggression occurred between a Blue-winged Warbler and a Lawrence's Warbler, singing Blue-wing song; a Golden-winged Warbler was aggressive toward both Blue-winged and Golden-winged warblers; and the Blue-winged Warbler attacked by the Golden-winged Warbler became aggressive toward that Golden-winged Warbler.

As the rare species becomes commoner, the frequency of hybridization could decrease as birds have a greater opportunity to develop species-specific responses and to find conspecific mates, although when progeny

of mixed matings are viable the initial noise in the system could persist for some time, if not indefinitely.

The hybridization of *Passerina* (Emlen et al. 1975) contrasts with that of *Vermivora*. Indigo Buntings (*P. cyanea*) and Lazuli Buntings (*P. amoena*) are not responsive to heterospecific song where allopatric, but they are where sympatric. And, whereas Blue-winged and Golden-winged warblers maintain overlapping territories with little conflict, the buntings and their hybrids maintain mutually exclusive territories. Nevertheless, Emlen et al. (1975:170) developed a model similar to ours: "that an individual bunting's behavior, upon hearing a heterospecific song, is determined by its prior behavioral experience with birds of the opposite species or song type." They also suggested (p 171) the possibility of "the existence of 2 separate processes in the ontogeny of bunting song: one associated with learning song *utterances* and another with song *recognition*" (emphases theirs).

Curiously, Emlen et al. (1975:172) concluded that response to heterospecific individuals, in places where the 2 species hybridize, is selected for because "we believe that this 'misidentification' is adaptive in promoting the establishment and maintenance of interspecific territories," contrary to the assumption of Murray (1971) that interspecific territoriality is most often misdirected intraspecific territoriality, resulting when 2 species share similar features that stimulate intraspecific territorial aggression, because of common ancestry, convergence, or accident. Interspecific territoriality between males of hybridizing populations seems most clearly to be the result of errors in the development of species-specific responses to both species-specific and non-species-specific stimuli.

We have generalized an observation into a model of the ontogeny of species discrimination. However, we also recognize that, just as the ontogeny of vocal development ranges from birds which develop species-specific vocalizations without hearing conspecifics, to birds which normally copy songs from conspecifics (Konishi and Nottebohm 1969), species discrimination may sometimes develop in birds without contacting either conspecifics or heterospecifics and may sometimes develop as a consequence of complex interactions between a bird and other individuals, conspecifics, heterospecifics, or both.

SUMMARY

We studied populations of color-marked Blue-winged, Golden-winged, Brewster's, and Lawrence's warblers at 2 places in south-central Michigan in 1969, 1970, and 1971. The birds arrived in late April or early May, but some individuals appeared on and competed for territories as late as early June. Arrival dates for the species broadly overlapped with only a few Blue-winged Warblers appearing before the earliest

Golden-winged Warblers. The territories of Blue-winged and Golden-winged warblers broadly overlapped in habitats occupied by both species. As expected from playback experiments most individuals discriminated, or at least did not respond to, the other species. Few birds were persistently interspecifically aggressive.

The intraspecific and interspecific aggressive behaviors of these warblers are described in some detail. They are characterized by their diversity in duration, intensity, and associated vocalizations. The interactions between a Blue-winged Warbler and a Golden-winged Warbler with Blue-wing Type I song proved of particular interest. We suggest the possibility that the development of species discrimination in males involves, in part, the kinds of responses the birds generate in other birds.

ACKNOWLEDGMENTS

We are grateful to Paul Wiggs and to Gordon Zorb, respectively, for allowing us to conduct our studies at the Island Lake Recreational Area and the Rose Lake Wildlife Research Area. Gill's participation was supported by a grant from the Society of the Sigma Xi.

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